hand statement that we see simply clouds floating in the atmosphere of the planet.

G. W. HOUGH.

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*THE ORIGIN OF TERRESTRIAL PLANTS.**

I SHOULD like to invite your attention for a little while to some of the factors that apparently have been operative in determining the changes which plant structures have undergone in the course of the development of the vegetable kingdom. While some of these are perfectly obvious, others are by no means so evident, and, as might be expected, there is not perfect agreement among botanists as to the relative importance of some of these factors, nor indeed of their efficiency at all.

I shall not attempt here to go into any extended discussion of the remarkable results obtained by Professor De Vries in his recent studies upon variation in plants. These are too important, however, to be dismissed without some mention. The conclusion reached by Professor De Vries is that, in addition to the variation within the limits of species, there may be sudden variations, or 'mutations,' which, so to speak, overstep the limits of the species, and thus inaugurate new species. While the results obtained, especially in the case of *Œnothera Lamarckiana,* are certainly most striking, more data are necessary before we can accept without reserve the conclusions reached. It is certain that marked changes—'sports,' as the gardeners term them—often appear without any explainable cause, and it is equally difficult to understand, what for want of a better term, we can only term 'tendencies' to develop in special directions. Thus the specialization of the sexual reproductive cells, which has evidently taken place quite independently in several unrelated lines; the development of heterospory, and probably of the seed-habit in different groups independently, are hard to explain without assuming an innate tendency to vary in a determined direction.

It is not, however, with these exceedingly difficult and often obscure problems that we shall concern ourselves here, but rather with those changes in plant structures which are referable to more or less evident response to known conditions.

Speaking in broad terms, I think we can reduce the determining factors to three categories, leaving aside the inherent tendencies to variation. These three sets of factors are: (1) those relating to the food supply, (2) the relation to water and (3) those concerned with reproduction.

It is hardly necessary to say that there is no fundamental distinction between plants and animals. At the bottom of the scale of organic life are many forms, especially those belonging to the group of Flagellata, which are intermediate between the strictly animal and vegetable organisms.

We may safely assume that the primitive organisms were motile, perhaps resembling some of the existing flagellates. Of the latter some are destitute of pigment and approach the lower Protozoa; others are provided with chromatophores containing chlorophyll and resemble the lower plants. It is highly probable that the forms with chromatophores are able to assimilate carbon dioxide, as the typical plants do, and may be denominated 'holophytic.' The forms without chlorophyll are probably, like animals, dependent upon organic food for their existence.

If we compare the holophytic flagellates with those forms which have no chlorophyll, a significant difference may be noted, which is evidently associated with

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their nutrition. The holophytic forms are noticeably less motile than the others. Thus *Euglena*, one of the commonest green flagellates, becomes encysted before division takes place. The resting cell has a firm membrane about it, and closely resembles a typical plant cell. The forms without chromatophores, however, *e. g.*, *Scytomonas*, may divide longitudinally in the active condition. This difference in motility between the forms with and without chromatophores seems to be the first hint of the differentiation of the characteristically motile animals and immobile plants.

One group of plants (Volvocaceæ) evidently allied to the Flagellata, and sometimes even included with them, like animals, show active locomotion during their vegetative existence. Aside from these, and the Peridineæ, which may be remotely related to them, locomotion is exhibited only by such reproductive cells as zoospores and spermatozoids. The frequent reversion to the motile condition found in the reproductive cells suggests the probability that these have been derived from similar ancestral forms.

The loss of motility in typical vegetable cells is associated with the formation of a firm membrane, usually of cellulose, about the cell. This precludes all movement of the cell, except in those cases where openings are present, through which extensions of the protoplasm, usually in the form of cilia, protrude.

The power of free locomotion was probably a character of the primitive vegetable cell, but with the development of the holophytic habit, this power has been lost by the vegetative cell of most plants. The loss of locomotion in plants may probably be connected with the development of the power to assimilate carbon dioxide, the main source of food. As the CO_2 in the air, or dissolved in water, is constantly being received, it is not necessary for the plant to move from one place to another in search of food, and we find plants becoming more and more stable. Where animals are so placed that their food supply is abundantly received, they may assume an immobile plant-like habit. This is especially marked in many marine animals, such as corals, hydroids, sponges, ascidians and such molluscs as oysters. The old name 'zoophyte' applied to corals and similar animals was not in all respects a misnomer. These rooted marine animals exhibit another resemblance to plants in the development of free swimming larvæ, analogous to the active zoospores produced by so many algæ. In both instances it is safe to assume that the motile stage is older than the fixed condition.

Lack of time forbids our consideration in detail of the very important, but by no means clearly understood, problems dealing with the evolution of sex in the vegetable kingdom. Thus the reason why the development of distinct sexual cells has taken place in an almost identical manner in several widely separated groups of plants is hard to explain. The sexual cells, or gametes, have beyond question been derived from non-sexual ones. Thus in several groups of algæ; *e. g.*, Volvocaceæ, Confervoideæ and Phæophyceæ, there still exists an almost perfect series of forms leading from the non-sexual zoospores to perfectly differentiated male and female gametes. The formation of sexual or non-sexual reproductive elements is, in many cases at least, largely dependent upon the conditions under which the plants are grown. This has been very clearly shown by the remarkable series of investigations made by Professor Klebs upon various thallophytes. For a discussion of the meaning of sex, the reader may refer to the recent papers on the subject by Strasburger and Beveri.

In short, while we know to a considerable extent some of the factors which determine the formation of sexual cells, where these have already been developed, the reasons why sex has developed are still very obscure.

Secondary reproductive structures, such as sporangia, seeds, flowers, fruit, etc., are readily enough explicable and need not be dwelt upon here.

PHOTOSYNTHESIS.

Perhaps the most important physiological property of green plants is the photosynthesis, or the ability to utilize the energy of the sun's rays for the manufacture of the primary carbon compounds necessary to build up living protoplasm. That some of the most striking modifications of the plant body are directly associated with photosynthesis is certain. The development of leaves in various groups of plants is, perhaps, the most obvious response to the needs for photosynthesis. The leaf is, *par excellence,* the photosynthetic organ. The spreading out of the green cells so as to offer the most favorable exposure to the light rays, and in the higher plants the development of stomata and the spongy mesophyll, or special assimilating tissues, are especially perfect. Leaves are by no means confined to the vascular plants, however. We need only recall the simple leaves of mosses and liverworts and the similar organs in the more highly organized seaweeds, such as *Sargassum* or *Macrocystis.* Even among the truly green algæ simple photosynthetic organs may be developed. The dense branching tufts of *Draparnaldia* or the expanded frond of *Ulva,* for example, are of this nature.

The leaves of these lower plants are very different morphologically from those of the ferns and seed plants, but show very clearly that they are physiologically of the same nature; *i. e.,* they are *analogous* but not *homologous.*

Other special modifications associated with photosynthesis are the peculiar lacunar tissues found in the thallus of the Marchantiales and in the sporogonium of the true mosses and in *Anthoceros.* In all these instances there are formed, in connection with the green lacunar tissue, more or less perfect stomata. These upon the apophysis of the sporogonium of many mosses, and over the whole surface in *Anthoceros,* are precisely similar to those found upon the leaves and other green organs of the vascular plants.

While it is usually stated that, among the bryophytes, appendicular organs are quite absent from the sporophyte, the apophysis, or special assimilative organ at the base of the capsule in some of the more specialized mosses like *Polytrichum* and *Splachnum,* might almost be so regarded. In the latter genus it sometimes forms a broad disk several times the diameter of the rest of the capsule, and is just as truly a special organ for photosynthesis as is the leaf of a fern or flowering plant.

WATER.

Even more important than the changes of the plant body associated with photosynthesis are those which are due to the plant's relation to the water supply. All organisms require a certain amount of water in order that the protoplasm may perform its functions. Protoplasm is not necessarily killed by the withdrawal of water, but it is rendered inactive, as may be readily seen in such structures as seeds, spores, etc.

The lowest organisms, whether plant or animal, are virtually aquatic; for, although they do not necessarily always remain in a liquid medium, they become quiescent when moisture is withheld. Very many, like most algæ, are true aquatics, and it

is safe to assume that the progenitors of the higher plants lived in the water. The nearest approach to these ancestral forms which have survived are probably certain green algæ, which have retained much of their primitive simplicity. Much the greater number of living plants, however, have given up the primitive aquatic habit for life on land. In adapting themselves to this new habitat they have contrived to exist with a much diminished water supply, which has enabled them to outstrip the much simpler forms which have retained their old aquatic habit.

The change from the primitive aquatic condition to the much more varied conditions of terrestrial existence is bound up with profound changes in the organization of the plant body.

MARINE PLANTS.

Of the existing plants which have retained the primitive aquatic habit, the most important are the various types of marine algæ, including not only the larger seaweeds, but also the minute pelagic forms like the diatoms and Peridineæ. Many of the larger seaweeds are very much better developed than the simple green fresh-water algæ, and show many special modifications associated with their peculiar environment. Not being subject to the drying up which threatens all fresh-water organisms at times, it is very rarely that marine algæ develop any form of resting-spores such as are so common among fresh-water algæ. On the other hand, those which grow between tide-marks, where they are regularly exposed at low-tide, develop mucilaginous or gelatinous tissues, which prevent too complete loss of water. This is especially well seen in the large kelps and similar forms. Some of these, also, reach an enormous size, and develop leaves which are often provided with bladder-like floats, which bring them to the surface when they are exposed to the light.

Very characteristic are the minute pelagic plants, especially the diatoms and Peridineæ, which are important constituents of the plankton, or surface life of the sea. These floating plants are generally provided with some sort of buoyant apparatus, evidently an adaptation to their pelagic life. Small as these floating algæ are individually, they are immensely important to ocean life, as they constitute the main source of food for the hosts of animals inhabiting the sea.

The great subkingdom of fungi offers many interesting problems bearing upon the evolution of plant-forms, but there is no reason to suppose that any higher types of plants have ever arisen from the fungi, many of which are doubtless plants of comparatively recent origin. Most of their peculiarities are associated with their nutrition, which is entirely different from that of typical plants. Not having chlorophyll, they are, like animals, dependent upon other organisms for food. Consequently all fungi are either saprophytes, living upon dead organic matter, or as parasites they attack living animals and plants.

I can not dwell here upon the extremely difficult problems connected with the origin and affinities of the fungi, even if I felt competent to discuss them.

THE ORIGIN OF TERRESTRIAL PLANTS.

We have now to consider what causes led to the abandonment of the aquatic habit by the algæ ancestors of the vascular plants, and how this radical change in their environment has influenced the development of the structures of the higher plants.

Nearly all fresh-water plants are exposed to destruction at times, by the drying up of the bodies of water in which

they live, conditions which are never met with in the life of most marine organisms. This necessitates some means of surviving the periods of drought, and has resulted in the development of various devices for carrying the plants through from one growing period to another. While a few low aquatics, like *Pleurococcus* or *Oscillatoria,* may become completely dried up without being killed, in most fresh-water algæ there are produced special cells—spores—which are more resistant than the vegetative cells and survive the death of the rest of the plant body. These resting spores may be produced non-sexually, as in *Nostoc,* or the 'aplanospores' of some of the green algæ; but more commonly they are the product of the union of sexual cells, or gametes, and may be generally denominated 'zygotes.'

This condition of things of course precludes growth, except when an abundant water supply is provided. It is evident that any device by which the vegetative life of the plant can be prolonged is an obvious advantage.

Some such contrivances, of a simpler kind, are seen in some of the lower green plants. Thus the gelatinous mass in which the filaments of a *Nostoc* colony are imbedded, or the 'palmella-stage' of some Confervoideæ, offer a certain amount of resistance to the loss of water, and serve to prolong the period of vegetation. Less commonly root-like organs are developed which enable the alga to live on the wet sand, penetrating into it and drawing up water from below. Species of *Vaucheria* and *Botrydium* exhibit this very well.

We may imagine that some algal form, perhaps related to the existing Confervoideæ, adopted a similar amphibious habit, developing rhizoids, by means of which it could vegetate in the mud after the subsidence of the water in which it was growing, in a manner analogous to that exhibited by certain amphibious liverworts still existing. The well-known *Ricciocarpus natans,* for example, lives first as a floating aquatic, but may later settle in the mud, as the water subsides, and there vegetates much more luxuriantly than in its aquatic condition.

The change from a dense medium like water to the much rarer atmosphere necessitates the development of mechanical tissues, to give the plant the requisite support in the air. There must also be developed devices for protecting the tissues against excessive loss of water due to transpiration. Other modifications are to insure economy of water in fertilization.

In submerged aquatic plants water is absorbed directly by all the superficial cells, and of course there is no loss due to transpiration. Moreover, special conducting tissues are made less important, and are either quite wanting, as in most algæ, or much less developed than in related terrestrial forms. As soon as a plant becomes terrestrial there must be provided organs (roots or their equivalent) for drawing up from the earth water to replace what is lost by transpiration, and in all but the simplest forms special conducting tissues to facilitate its transport. In the lower types of land plants, the absorptive organs are usually simple hairs (rhizoids), but these are quite inadequate to supply a plant of large size, and consequently it is only those terrestrial plants which are provided with a true root system that have succeeded in reaching a large size. Even in the lower terrestrial forms the rhizoids do not monopolize the absorption of water, but many of them are able to absorb water directly through the leaves or through the superficial cells of the thallus. While this is especially marked in many mosses and liverworts, which are, so to speak, more or less aquatic in their behavior toward water, it is by no means

confined to them, as most vascular plants develop structures, seeds, tubers, bulbs, etc., which can absorb water directly. Less commonly the leaves of vascular plants have this property. This is especially marked in various xerophilous plants, such as the Californian gold-back fern (*Gymnogramme triangularis*), *Selaginella rupestris* and other species, many species of *Tillandsia*, etc.

As all botanists know, the structural differences between aquatic and terrestrial plants are very marked, but there are some transitional forms which illustrate very beautifully the change from one to the other, and the efforts of the plant to adjust itself to the changed conditions. Thus some plants which are usually strictly aquatic, such as some water-lilies, may assume a nearly terrestrial condition, the long-stalked, floating leaves being replaced by those borne upon shorter upright petioles.

The primitive aquatic plants are either unicellular or simple cellular plants with relatively little differentiation of parts, as might be expected in organisms living in a relatively uniform medium. A necessity for their active existence is an abundant water supply, as they are not provided with any adequate means for resisting desiccation, although the mucilaginous or gelatinous substances in which their cells are sometimes imbedded serve to retard for a short time the loss of water by evaporation when they are exposed to the air. A good many of the lower fresh-water organisms are capable of becoming dried up without losing their vitality, but of course their activity is stopped. More commonly they depend upon special resting cells, or spores, to carry them through periods of drought or cold.

In exceptional cases, the lower algæ may assume an amphibious habit, living upon wet mud instead of actually in the water. *Botrydium* and some species of *Vaucheria* develop a simple root system by which the loss of water by transpiration is made good so long as the soil remains moist; but these quickly die as soon as the mud dries, as their cells are not protected against loss of water by evaporation.

It is, however, among the bryophytes, or mosses, that anything approaching a satisfactory solution of the problem of a terrestrial existence is attained. (I am leaving out of account the fungi.) All of the mosses are, to a certain extent, amphibious, since all of them require first water in order that fertilization may be effected. A small number, *e. g.*, *Riccia fluitans, Riella, Fontinalis*, etc., are genuine aquatics, and the life history of such a form as *Ricciocarpus natans* illustrates what has probably been the origin of the terrestrial habit in the primitive archegoniates. *Ricciocarpus* is usually a floating plant, but it not infrequently assumes a terrestrial habit, sometimes preliminary to developing its reproductive organs. This is brought about by the subsidence of the water until the plant is left stranded on the sand. Under such circumstances it grows very vigorously, develops numerous rhizoids which penetrate the mud and supply it with water. Excessive loss of water is checked by the development of a cuticularized epidermis covering the exposed surface of the thallus. It is highly probable that in some such way as this the algæ ancestors of the first archegoniate plants began their life on land, and slowly emancipated themselves from the necessity of being surrounded by water, and of course thus became more and more independent of the drying up of shallow bodies of water in which they grew. In this way the vegetative period would be much prolonged, and would give the plant a great advantage

over its aquatic competitors, and thus the terrestrial habit was established.

Some liverworts and mosses may reach considerable size, a foot or more in length in a few cases. They also exhibit a certain amount of specialization, corresponding to the requirements of the terrestrial environment. Well-developed leaves are present in nearly all true mosses, and in many liverworts, and in one order of the latter, the Marchantiales, the plant body, while retaining its thallose character, develops a complicated assimilative tissue, with stomata of a peculiar type not found elsewhere. In the upright forms mechanical tissues are developed, and in the true mosses there is present in the leafy shoots a central strand of conducting tissue, comparable to the vascular bundles found in the sporophytes of the vascular plants. Indeed the analogies existing between the leafy moss-shoot and the sporophytic shoots of the vascular plants are sufficiently obvious.

No existing bryophytes have succeeded in reaching any but the most modest dimensions. All the larger forms either are prostrate or grow in dense tufts, offering mutual support to the leafy shoots. Indeed no moss seems to have quite solved the problem of a self-supporting upright leaf-supporting axis. Neither have they successfully solved the problem of an adequate water supply, to compensate for loss of water by transpiration, and this of course is closely associated with the limit of size which the plant-body could assume. Given an unlimited water supply, and a plant, even of low organization, may attain very large dimensions, as we see in the giant kelps. Those plants, although in many respects of very low rank, nevertheless may reach hundreds of feet in length, and develop specialized tissues, curiously suggesting those of the highly organized land plants. These giant seaweeds absorb water throughout their whole superficial area, and there is no loss of water by transpiration; but for a terrestrial plant to reach a large size there must be adequate means for absorbing water from the soil, and for transporting it expeditiously through the plant to those places where water is being lost through transpiration.

In the highest terrestrial plants, the 'vascular' plants, we meet first with a perfect system of water-conducting tissue. This is the woody portion of the fibro-vascular bundles, composed of the characteristic tracheary tissue, first encountered in the ferns, and common to all the higher plants.

ORIGIN OF THE SPOROPHYTE.

Among the lower terrestrial plants, the Archegoniatæ, which comprise the mosses and ferns, a very marked characteristic is the 'alternation of generations.' By this is meant that in its development the plant passes through two very different phases, a sexual and a non-sexual one. This is perhaps best seen in the ferns. The spore of the fern, on germination, gives rise not to the leafy fern plant, but to a much simpler plant much like a small liverwort, upon which the sexual reproductive organs, the archegonium and antheridium, are borne. This sexual plant is known as the gametophyte. Within the archegonium is borne the egg-cell or ovum, which, after being fertilized, ultimately produces the leafy fern plant, or 'sporophyte,' from its producing the spores, or non-sexual reproductive bodies.

Among the lower Archegoniates, the gametophyte is relatively much more important, and the sporophyte is never an independent plant, as it is in the ferns, but always remains to a greater or less extent dependent upon the gametophyte for its existence.

An alternation of generations is hinted at among some of the green algæ, but never becomes sharply defined as it is in the archegoniates. Among the red algæ, however, it becomes clearly marked, and also in many fungi. In both of the latter cases it is extremely probable that we have to do merely with analogies, as there is not the slightest evidence of any genetic connection between either of these groups and the archegoniates.

With the green algæ, however, the case is somewhat different, and it is highly probable that the earliest archegoniates arose from some forms not very different from *Coleochæte,* a green alga in which the fertilized egg gives rise to a very simple sporophytic structure.

The increase in the output of the zygote, or fertilized egg, due to its division into a number of spores, instead of forming at once a single new individual, is an evident advantage which becomes increasingly important as the gametophyte assumes the character of a terrestrial plant, and the chances of fertilization, which requires the presence of water, become correspondingly lessened.

There are two theories as to the origin of the alternation of generations among the archegoniates, the 'homologous' and 'antithetic.' The first holds that the non-sexual sporophyte is a direct modification of the gametophyte and probably arose from it as a vegetative outgrowth. The antithetic theory holds that the sporophyte always, in normal cases, arises from the fertilized ovum, and is a further development of the zygote which has arisen in response to the requirements of a terrestrial existence. There is not time here to consider at length the relative merits of these two theories. In a special paper before the section, I hope to bring this matter up for discussion. For present purposes I shall assume that the latter (antithetic) view is the correct one.

As the ancestors of the archegoniates left their original aquatic habitat, the question of the water supply became of the first importance. All of these lower land plants have retained many of their original characteristics, among them the development of motile male cells (spermatozoids), which require free water in order that they may reach the egg-cell and fertilize it. That is, the plants are, to a certain extent, amphibious, and must return to the water in order that fertilization may be effected. It is very clear, then, that anything which tends to increase the number of spores resulting from the developed zygote will be advantageous, rendering a single fertilization more and more effective.

The alternation of sexual and non-sexual plants among the green algæ is not sharply marked, and has been shown to be largely a matter of nutrition. Nevertheless, as already mentioned, there is a hint of an alternation of generations in certain forms like the higher Confervoideæ. In these the germinating zygote produces a larger or smaller number of zoospores, which give rise to as many new individuals. From some such form as these in all probability the primitive archegoniates arose. As these became distinctly land plants, the motile zoospores resulting from the zygote of the algæ gave place to the non-motile spores characteristic of the terrestrial archegoniates; but of any transitional forms we are quite ignorant, and the gap between algæ and archegoniates is a very deep one.

The gradual specialization exhibited by the existing liverworts and mosses is familiar to all botanists, and will only be briefly discussed here. Enough to say that from the simplest type, a globular mass of spores, with almost no sterile tissue developed, such as occurs in the Ricciaceæ, there are

still found almost all intermediate conditions, culminating in the large and complex sporangia of the true mosses, and the somewhat similar but much simpler one of *Anthoceros.*

In following such a series it is clear that spore-production, the sole function of the primitive sporophyte, becomes largely subordinated to the purely vegetative existence of the sporophyte. Thus in such a moss as *Polytrichum,* the sporogenous tissue does not appear until a late period in the development of the sporophyte, and comprises but a very small fraction of its bulk. An elaborate system of assimilative tissue, with lacunar green tissue and stomata like those of the vascular plants, is developed, and the loss of water due to transpiration is made good by a strand of conducting tissue, which represents a simple type of vascular bundle.

While the elaborate sporophyte of the mosses offers certain suggestions of the structures of the vascular plants, it is much too highly specialized in other directions to make it in the least probable that it has given rise to any higher forms. The equally dependent but much simpler sporophyte of the peculiar group of the Anthocerotales is probably very much more like the forms from which this independent sporophyte of the ferns arose than is the more highly developed sporogonium of the true mosses.

The subject of the gradual elaboration of the sporophyte cannot be dismissed without reference to the very important work of Professor Bower, whose clear exposition of the progressive sterilization of the tissues of the originally exclusively sporogenous sporophyte is one of the most important contributions to the subject.

When we review the extraordinarily large number of resemblances between both gametophyte and sporophyte in the ferns and liverworts, the weight of evidence, to my mind, is overwhelmingly in favor of assuming a real genetic connection between the two groups. To say 'that no structures among plants seem to have left so little trace of its origin as do the leafy sporophytes of Pteridophytes and Spermatophytes,' is certainly to ignore all the principles of comparative morphology. When we reflect that the reproductive organs and mode of fertilization are the same in all archegoniates; that the early divisions and growth of the embryo are identical; that in the more specialized bryophyte the sporophyte develops assimilative and conductive tissues strictly comparable to those of the Pteridophytes; and finally, that the spore formation is identical to the minutest details; surely such a statement is very far indeed from stating the truth.

The fallacy of the arguments based upon apogamy has been ably refuted by Professor Bower. He has called attention to the fact that nearly all cases of apogamy are abnormal, and occur in forms where the sporophyte normally is produced from the egg. It is also noteworthy that the greater number of cases of apogamy occur in extremely variable species, such as the crested varieties of different ferns (*e. g., Scolopendrium vulgare* var. *ramulosissimum*). Professor Bower has also called attention to the fact that these are all forms belonging to the highly specialized and relatively modern group of Leptosporangiatæ. If apogamy is a reversion to a primitive condition, it is strange that it should occur in the least primitive ferns rather than in the older types.

I think we may fairly class the phenomena of apospory and apogamy with the numerous cases of adventitious growths so common among both pteridophytes and seed plants. In these the whole sporophyte may originate as a bud from any

part of the plant. Such adventitious shoots may arise from leaves, as in many ferns, *Begonia, Bryophyllum,* etc.; from roots, in *Ophioglossum,* and many seed plants, *e. g., Populus, Robinia, Anemone,* etc., or even from sporangia, as in the budding of the nucellus of the ovule recorded in several cases of polyembryony. Now, no morphologist would argue from these that they are in any sense reversions, and I can not see why the case of apogamous, or aposporous budding is essentially different.

No bryophytes have quite emancipated themselves from the aquatic habit of their algal progenitors. While they may often dry up for an indefinite period without being killed, there is, nevertheless, much of the same dependence upon an ample water supply that we find in the algæ. Although much more resistant to loss of water through transpiration than are the few terrestrial algæ, nevertheless the bryophytes, as a rule, are much less suited to a genuine terrestrial habit than are the vascular plants. Much the same means are employed by many bryophytes in the absorption of water as by the algæ. Water may be absorbed by all the superficial cells, the roots playing a minor rôle as absorbents, except in those forms in which the plant is a prostrate thallus, where roots are often developed in great numbers. These delicate rhizoids, however, would be quite inadequate to supply the needs of a leafy stem of any but the most modest proportions. In a few bryophytes, *e. g., Chimacium,* there are rhizome-like modifications of the shoot, which may to a limited degree be compared to roots, but any proper roots, like those of the vascular plants, are quite absent. It would seem as if nature's attempts to adapt the originally strictly aquatic gametophyte to a radically different environment had been only partially successful, owing to the failure to develop an adequate root system to restore the water lost through transpiration. It may be that the range of variation any structural type may undergo is limited.

If we accept this hypothesis, it may help to explain the significance of the alternation of generations as developed among the archegoniates, and we can understand why the sporophyte has gradually replaced the gametophyte as the predominant phase of the plant's existence. Attention has already been directed to the perfectly well-known fact that sudden marked variations may appear in plants without any apparent cause. The work of De Vries emphasizes this, and refers all radical advances in structures to such mutations, which are clearly distinguished from the variations which occur within the limits of a species, but which can not apparently overstep certain limits.

In accordance with this view it is quite conceivable that the first appearance of the leaf upon the sporophyte may have been comparatively sudden—that is, there may not necessarily have been a long series of preliminary structures leading up to a true leaf.

It has been urged that the antithetic theory of the nature of the sporophyte involves the sudden appearance of a new structure. The fallacy of this claim has been pointed out by Professor Bower, and a little thought will show that no claim is made of the sudden appearance of a new structure. While no strictly intermediate forms are known, there is certainly no difficulty in seeing the essential homology between the rudimentary sporophyte of such an alga as *Coleochæte* and that of *Riccia.* The antithetic theory merely claims that the structure developed from the zygote, which at first is devoted exclusively to spore formation, gradually develops vege-

tative tissue as well, and finally attains the status of an independent plant.

The highly organized sporophyte of the higher archegoniates is connected with the lower types by an almost continuous series of existing forms, and through these with the still simpler structures found in the green algæ. The increased output of spores, with a corresponding number of new plants resulting from a single fertilization, is an obvious advantage, and undoubtedly is the explanation of the origin of the sporophyte.

If we compare the sporophyte of even the simplest liverwort with that of the algæ, there is noted an essential difference. The spores, instead of being motile zoospores, are non-motile, thick-walled structures, adapted to resist drying up—in short, the sporophyte is a structure essentially fitted for an aerial existence. Except in the very lowest types, there is developed a special massive absorbent organ, the foot, which is not unlike the root developed in the higher types, and is very different from the delicate rhizoids of the gametophyte. The latter always shows, to a greater or less degree, its aquatic origin.

From the time that the sporophyte has attained the dignity of an independent existence, its development proceeded on lines very different from those followed by the essentially aquatic gametophyte. As we have seen, the efforts of the latter to assume a terrestrial habit have met with only partial success, and it would appear that nature concluded to try again, taking as a starting point the essentially terrestrial sporophyte, which, as a functionally new development, seems to have proved more plastic than the gametophyte.

From the first, and this I believe to be highly significant, its water supply was obtained indirectly through the medium of a special organ, the foot. It is not important for a consideration of the question whether the foot in all forms is or is not homologous—enough that we find for the first time an organ sufficiently massive to supply all the water needed by the tissues of the developing sporophyte. The foot is a very different organ from the delicate rhizoids of the gametophyte, and much more like the true roots of the vascular plants, which, it is highly probable, arose as further modifications of the foot of the sporogonium of some bryophyte.

With the massive root penetrating the earth and thus establishing communications with the water supply, the sporophyte becomes entirely independent. The possession of an apical meristem in the root allows of unlimited growth, and gradually the massive root system of the higher plants has been evolved, keeping pace with the increase in size of the sporophyte, which, except with rare exceptions, obtains its whole water supply through the roots. Correlated with this increase in size of the sporophyte has been developed the characteristic conducting tissues which constitute the vascular bundles. While rudimentary vascular bundles are found in the sporophyte of many mosses and in *Anthoceros*, the characteristic tracheary tissue, *par excellence* the water-conducting tissue of the vascular plants, occurs only among the latter forms.

With the establishment of the sporophyte as an independent plant, the gametophyte serves mainly to develop the sexual reproductive organs from which the sporophyte arises. While the gametophyte among the lower pteridophytes is a relatively large and independent green plant, sometimes living for several years, it becomes much reduced in size among the more specialized heterosporous types, and may live but a few hours, as in species of *Marsilia*. In such forms little or no chlorophyll is developed by the gametophyte, which depends for its growth upon

the materials stored up in the spore, or even lives parasitically upon the sporophyte, as in *Selaginella,* thus reversing the relation of sporophyte and gametophyte found in the lower archegoniates.

All of these modifications are in the direction of economy of water, in accord with the needs of a more and more pronounced terrestrial habit.

Just as heterospory arose independently in several groups of pteridophytes, so also the seed habit—the final triumph of the terrestrial sporophyte over the primitive aquatic conditions—developed more than once. The female gametophyte, included within the embryo-sac, develops without the presence of free water, and the germinating pollen-spore also absorbs the water it needs from the tissues of the pistil, through which the tube grows very much as a parasitic fungus would do. Except in a very few cases, the male cells of the seed plants have lost the cilia, the last trace of their aquatic origin, and are conveyed passively to the egg-cell by the growth of the pollen-tube.

Once firmly established as terrestrial organisms, and the problem of water supply solved, the further development of the seed plants is too familiar to need any special comment here. The great importance of water in affecting the structure of land plants is seen in the innumerable water-saving devices developed in the so-called 'xerophilous' plants, seen in its most extreme phase in such desert plants as cacti, or in the numerous epiphytes, like many orchids and bromeliads.

In short, it is safe, I think, to assert that of all the extrinsic factors which have affected the structure of the plant body, the relation to the water supply holds the first place. The most momentous event in the development of the vegetable kingdom was the change from the primitive aquatic habit to the life on land which characterizes the predominant plants of the present.

Douglas Houghton Campbell.

SECTION A, MATHEMATICS AND ASTRONOMY.

Vice-President—Professor George Bruce Halsted, Austin.

Secretary—Professor Charles S. Howe, Cleveland.

Member of Council—Professor John M. Van Vleck.

Sectional Committee—Professor G. W. Hough, Vice-President, 1902; Professor E. S. Crawley, Secretary, 1902; Professor G. B. Halsted, Vice-President, 1903; Professor C. S. Howe, Secretary, 1903; Professor Ormond Stone, five years; Professor J. R. Eastman, four years; Dr. John A. Brashear, three years; Professor Wooster W. Beman, two years; Professor Edwin B. Frost, one year.

General Committee—Mr. Otto H. Tittmann.

Papers were read as follows:

Deflections of the Vertical in Porto Rico: Otto H. Tittmann, Superintendent U. S. Coast and Geodetic Survey.

Mr. Tittmann gave an account of some large deflections of the plumb line in Porto Rico. Their existence was first noted by Count Canete del Pinar, of the Spanish Hydrographic Commission, which extended a triangulation around the island, but the war or other causes prevented a verification by that commission. The Coast Survey, however, in the course of its surveys extended a triangulation across the island from San Juan to Ponce and proved their existence beyond question. These deflections are so great that they affect the cartographic representation of the island, and a mean latitude had to be adopted, with the result that the northern coast line, as now shown on the maps, had to be moved by half a mile further south and the southern coast line by the same amount further north than would have been the case if the astronomical latitude had been used.